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To scale or not to scale: a perspective on describing fish energy budgeting

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Conventionally, dynamic energy budget (DEB) models operate with animals that have maintenance rates scaling with their body volume, and assimilation rates scaling with body surface area. However, when applying such criteria for the individual in a population level model, the emergent behaviour of the conventional model apparently only reflects juveniles and not adult animals. This paper discusses the relevance of what level assumptions are made on, and the subsequent impact on interpreting the animal (top-down or bottom-up). The alternative DEB model has maintenance scaling with body area, and assimilation with body volume—the opposite of the conventional energy budget animal. Likewise, scaling of organism function to body mass is emphasized to take into account the different challenges organisms face when growing in size. It is emphasized that homeostasis and its challenges are continuously changing, and cannot be assumed constant. The perspective is finalized by a discussion on perceiving animals as machines, and how it can maybe serve as a *lingua franca* for physiologists and modellers alike.

Key words: Aerobic scope, dynamic energy budgeting, efficiency, fishes, gills, homeostasis

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Introduction

Assessing effects of perturbations (e.g. fisheries) on ecosystems requires a mechanistic approach in determining cause and effect relationships (Horodysky *et al.*, 2015; McKenzie *et al.*, 2016). For this purpose, organismal physiology has been suggested as a viable tool, as the environment, and the physiology of organisms continually interact (Clarke, 1993). Furthermore, since the dawn of physiology as a research topic, the field has expanded widely, leading Wieser (1973) to formulate a need for analytical approaches for the progression of the area.

‘Since the purely descriptive phases in the former sciences [biochemistry and physiology] have largely passed it is the application of strictly analytical methods that will lead to the formulation of the questions that are to occupy biochemists and physiologists of the future.’—W. Wieser, 1973

When an analytical model of any system is being coined, it is of importance how the system is perceived. In trying to describe an animal as a system, in words or via a mathematical model, from which perspective one perceives the animal will affect how one describes it. One fundamental difference in describing complex systems is whether one attempts to describe the system from a bottom-up or a top-down point of view (Pezzulo and Levin, 2016) (Fig. 1). A Bottom-up approach tries to describe the animal by its specific components and their responses, and as components are added complexity ensues. On the other hand, in a top-down approach, all the individual processes integrated as one, yielding a generalized response. Some 90 years ago, Krogh (1929) described that the physiology as ‘growing unwieldy,’ making it impossible for one person to be familiar with all branches, illustrating the complexity of physiology already at that time. When trying to

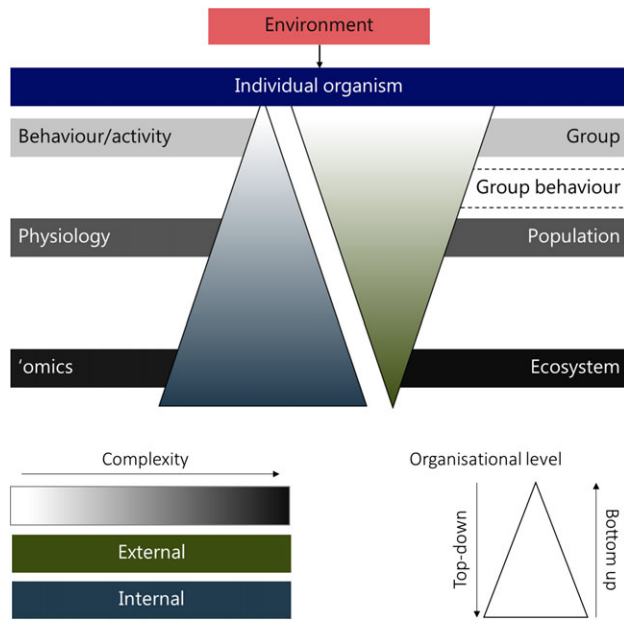


Figure 1: Perception of the animal. This diagram seeks to visualize organizational level of an organism in nature, as well as describing the relative complexity observed at different levels of life. Bottom left is the complexity scale, with colour codes signifying inner and outer environments. Bottom right is the organizational scale, based on degrees of freedom, i.e. how many things can vary, dependent on what scale a researcher observes life. 'Internal': Starting from the 'individual organism' and down the triangle, a top-down approach i.e. integrative physiology tries to describe the status of the animal looking at whole animal activity and its physiological status, (Fry, 1971). A bottom-up approach would be a reductionist method, seeking to describe the organism starting at a regulatory or gen'omic' level, moving up. The latter can prove difficult, if not impossible (Pezzulo and Levin, 2016), as the integrated complexity would increase closer to the bottom of the internal triangle. 'External': Group, Group behaviour, population and ecosystem are at a higher organizational level than the individual, as there logically fewer populations of fish than individual fish, as individuals make up the populations—likewise for populations vs. ecosystems. As more and more individuals are included going up the outside environment organization, more and more degrees of freedoms are added.

describe a system bottom-up, one has to make assumptions, in a way that sets the rules of life for the given description or model. The set of assumptions of a model defines the scope of application of the model and increasing the number of assumptions limits the applicability of the model. In the paper, 'A paradox in individual-based models of populations' by van der Meer (2016), the author highlights a paradox in the application of assumptions in conventional dynamic energy budget (DEB) models. The paradox is that in contrast to conventional DEB models, the desired behaviour of an alternative DEB model, created by van der Meer (2016) requires the creation of a 'weird animal' where maintenance scales with body area and assimilation rate scales with body volume.

In this perspective, the importance whole organism function and homeostasis are emphasized when analytically

describing physiology. Exemplified by highlighting what the authors perceive as an oddity in the assigning of functional scaling to a specific organismal dimension, rather than to assign it to a specific need or challenge. Finalized by a discussion on the usefulness as perceiving organisms as machines.

Different perceptions of fish energy budgeting

The cornerstone of physiology, both in the field and in the laboratory, is the concept of homeostasis; that animals maintain an inner environment optimal for processes of life (Cannon, 1935; Costa and Sinervo, 2004; Cooper, 2008). The concept of homeostasis is a general top-down perception in physiology, with the only rule being the active maintenance of organismal homeostasis to ensure organismal function. A bottom-up approach to how the 'environment' affects behaviour and distribution of animals is whole animal physiology and behaviour. Fry (1947, 1971) proposed a framework that relates environmental effects on whole animal metabolism to animal activities, such as growth and habitat selection, both of which will have a consequence for lifetime fitness. The determinant of habitat choice and growth potential have often, due to the works by Fry, been interpreted as the aerobic scope (AS), that is, the capacity of the animal to increase its oxygen consumption from resting level (Fry, 1971). As of present, however, there is an ongoing discussion of the practical applicability of the AS as a bottom-up approach to higher order analyses (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Clark *et al.*, 2013; Gräns *et al.*, 2014; Norin *et al.*, 2014; Brijs *et al.* 2015; Farrell, 2016).

Dynamic energy budget model theory: A potential gathering theory is the maximum power principle described by Lotka (1922a, 1922b) which suggests that natural selection acts on maximum available energy (Sciubba, 2011). In this context, it makes sense that animals can balance the different costs and gains attributable to an environment via metabolic resource allocation (Priede, 1985; Korsmeyer *et al.*, 1996; Holt and Jørgensen, 2015; Sandblom *et al.* 2016). This sub-organismal level of allocating energy (Kooijman, 1986) is closely related to the theory of DEB (Kooijman, 1986; van der Meer, 2006; 2016; Sousa *et al.*, 2008), and can at the same time explain the physical theory that underlies the Fry paradigm.

Homeostasis

A general top-down perception in physiology is the centring on homeostasis, with the only rule being that organismal homeostasis is maintained for organismal function. However, investigating parts of organisms and focusing on those parts' responses to challenges has been a general practice and is, in essence, a bottom-up approach: homeostasis is about keeping the mitochondria well-functioning. Simplified, this allows

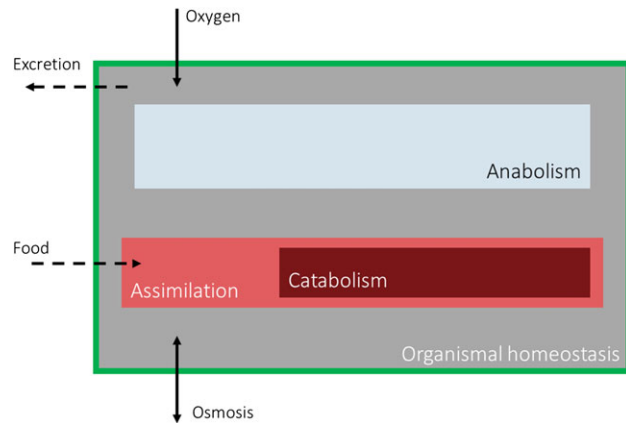
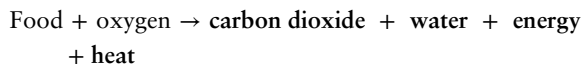


Figure 2: Energy budget of a resting fish. Organismal homeostasis, grey, is here depicted as 60% of the total expenditure (150 cm^2), the primary constituents being convective 'oxygen transport' (branchial + cardiac) and 'osmoregulation'. Behaviour and similar activities are not included here, as the fish is at rest. Assimilation of food to utilizable energy is represented in this situation at a level of $\approx 18.3\%$ of the total budget (27.5 cm^2), of which catabolism uses 45% (representative of Alanine) (Applebaum & Rønnestad (2004), Rønnestad *et al.* (2001)). Lastly anabolism, i.e. growth, consists of $\approx 22\%$ (32.5 cm^2). The given situation leaves room for growth in the sense of Von Bertalanffy (1934) since anabolism is larger than catabolism (assimilation). The green line represents any surface of the organism, where uptake of oxygen and exchange of water and ions occur.

thinking of animals open systems (Fig. 2), where different transport phenomena interact in maintaining homeostasis. Transport phenomena have been argued to be the cause of allometric scaling in biology (West *et al.*, 1997; Savage *et al.*, 2007). Oxidative phosphorylation that forms the core reactions of metabolism requires both substrate (food) and oxygen to take place. Respiration:



Oxygen is not a substrate that can be converted to a reserve; it needs to be taken up and utilized directly in metabolism. Therefore, oxygen homeostasis should be regarded as a primary organismal function; insufficient oxygen uptake will lead to anaerobiosis that in turn will be detrimental to all other homeostatic functions (Pörtner and Grieshaber, 1993). As a result, it seems fair to assume that the first costs to pay would be the most immediate for whole organism function, the ones associated with oxygen uptake, which is ventilation and cardiac oxygen transport (external and internal oxygen transport, respectively).

Any energetic part of organismal homeostasis would be included in what is known as the standard oxygen consumption (Beamish, 1964) (often described as Standard Metabolic Rate, SMR, as oxygen consumption is a proxy for metabolic rate when studying fishes (Fry, 1971; Nelson, 2016). The

standard metabolic rate would be the average maintenance cost of living for a resting fish (Beamish and Mookherjee, 1964; Beamish, 1964), and both energetic cost of ventilation and osmoregulation, therefore, are examples of homeostatic processes that must be considered a part of SMR (Fry, 1971). The metabolic cost of ventilation varies from 4 to 43% but is most likely in the vicinity of 10% in normoxia (Jones *et al.*, 1970; Jones, 1971; Jones and Schwarzfeld, 1974; Kramer, 1983; Steffensen and Lomholt, 1983). The cost of internal (cardiac) oxygen transport (Hughes, 1973), has as such not been assessed but suggested to equal that of ventilation (Jones, 1971; Farrell and Steffensen, 1987). However, considering the volumes of internal and external oxygen medium needing transport to maintain a fixed oxygen consumption, ventilation of water requires much larger volumes be moved compared to that of blood (Piiper *et al.*, 1971; Piiper and Scheid, 1984), why it logically could be assigned as the most costly.

A second abiotic factor affecting maintenance costs via the gills would be the cost of osmoregulation. Osmoregulation has been reported from in the order of a few percent, over 12–16% (Febry and Lutz, 1987) to as high as 50% (Febry and Lutz, 1987; Boeuf and Payan, 2001). However, the cost of osmoregulation seems to interact with temperature (Christensen *et al.*, 2017), why it is difficult to assign a single percentage. Summing up these two factors directly attributable to surface area, expected maintenance cost of the fish would range from a minimum of 20–30% to at least 60% of measurable maintenance metabolism (SMR). Both oxygen uptake and osmoregulation are challenges included in the whole organism homeostasis, and the gills are the major functional organ for both (Evans *et al.*, 2005).

Scaling

In the contemporary paper by Lefevre *et al.* (2017), gill surface-to-volume is argued to scale with an exponent of 1 with body mass. The arguments in Lefevre *et al.* (2017) claims against the gill scaling assumptions of Pauly *et al.*, yet in predictions of future size ranges of fishes, however, Lefevre *et al.* (2017) do not deny the many functions occurring in connection with the gills. Figure 3 illustrates that scaling of physiological entities with body size is largely dependent on the unit used to quantify them. The two top panels show SMR values from the dataset in Lefevre *et al.* (2017), as a function of body mass. Whole animal oxygen consumption, MO_2 , ($\text{mg} \cdot \text{min}^{-1}$) scales with an exponent of ≈ 1.2 , indicating that it increases faster than body mass alone. However, using mass-specific oxygen uptake ($\text{mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) to remove the effect of mass, then the scaling exponent becomes negative (≈ -0.13), indicating fewer costs per unit of mass for larger animals. Lastly, when correcting for temperature ($Q_{10} = 2$, 20°C) the effect of body mass on oxygen consumption decrease to ≈ -0.042 (Table 1). Just as well as oxygen uptake is an approximation on metabolism (Fry, 1971; Nelson, 2016), one could argue that ventilation is a

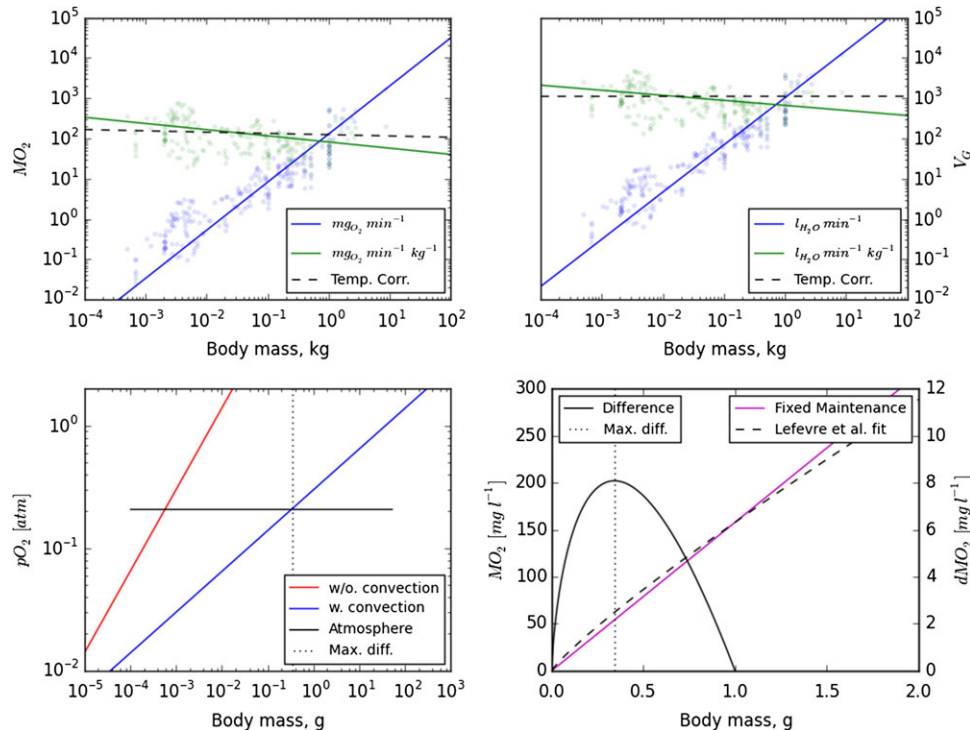


Figure 3: Top left: Oxygen consumption (MO_2) at standard metabolic rate of different fishes and conditions ($n = 218$) vs body mass in kg on the x-axis (data from Lefevre *et al.* (2017)). Demonstrates different scaling of MO_2 vs the mass of the animals, using either mass-specific [$mg \cdot min^{-1} \cdot kg^{-1}$] ($b = -0.154$) or whole animal oxygen consumption rates [$mg \cdot min^{-1}$] ($b = 1.196$), the dashed line represent a temperature correction of mass-specific scaling ($b = -0.042$). Top right: pane is similar to the top left, except oxygen consumption has been converted to ventilation [$l_{H_2O} \cdot min^{-1} \cdot kg^{-1}$] ($b = -0.125$; temperature corrected $b = -0.009$) and [$l_{H_2O} \cdot min^{-1}$] ($b = 1.172$). Bottom left: panel depict calculations of oxygen transport limitation of size in organisms relying on aquatic respiration, as per Krogh (1941). The x-axis with the units the units of mass in gram, assuming a sphere shape organism with mass scaling with $b = 1$ to volume. The intersection of the coloured lines with the horizontal black line, signifies where metabolism starts being limited by oxygen transport (0.21 atm) (red: diffusion only, blue: with convection/ventilation) (Krogh, 1941). Bottom right: depicts the fitted equation of metabolic rate reported in Lefevre *et al.* (2017), converted to whole animal oxygen consumption (—). The magenta graph represents a fixed metabolic rate (maintenance at body mass approximating 0 g) the difference between the two lines (—) and a vertical line (:) highlighting where the difference between fixed maintenance (magenta) and scaled maintenance (—) are the largest ($M_b \sim 0.32$ g). The dotted line in the bottom left represents the same point, e.g. maximum difference between the fitted equation from Lefevre *et al.* (2017) and that of fixed maintenance. For a body mass larger than the found $M_b \sim 0.32$ g, respiration of an aquatic organism requires further measures than convective oxygen transport only, e.g. haemoglobin, to increase the gradient across the gas exchanger (Krogh, 1941; Schmidt-Nielsen, 1984).

proxy for oxygen uptake. By correcting the oxygen uptake for the oxygen content of the ventilation medium, oxygen consumption can be expressed as ventilation volume, V_G , ($L \cdot min^{-1} \cdot kg^{-1}$). In doing this, the scaling exponent of ventilation with body mass becomes -0.009 , that is, practically constant.

In conclusion, the most determining factors in the order of impact for scaling of oxygen uptake in fishes are body mass, temperature and ventilation volume. Depending on the units used to express metabolism (maintenance) the observed allometric scaling changes from positive, to negative, to almost zero. Thus, instead of considering whether maintenance or similar scales with a surface or volume, efforts should be put in establishing the actual currency, or unit, for the specific functions. The challenges faced in different

environments goes back to either thermodynamic effects on metabolism (temperature), or homeostatic (maintenance) challenges attributable to the gill surface area (oxygen, salinity) (Evans *et al.*, 2005). Suggesting that the body surface that relates to maintenance cost in fishes is the gill surface, as also stated by Pauly (1981). That the gill surface also represents the largest working surface of the fish is additional support for this (Byczkowska-Smyk, 1957). Due to the large water transport in connection with oxygen uptake occurring over the gills, the gill surface inflicts homeostatic challenges on fishes (Evans *et al.*, 2005). As a consequence, maintenance costs scale to the metabolic rate and physical size of the organism. Scaling of maintenance via ventilatory volume sets an environmental dependency of homeostasis via the gills. If metabolic demand for oxygen is high, supply is low, or a combination, gills (surface) and heart (ventricular mass)

Table 1: Scaling exponents of fishes and the effects of unit conversion and transformation

Scaling exponents, <i>b</i>	Oxygen consumption		Ventilation	
	mg · min ⁻¹	mg · min ⁻¹ kg ⁻¹	L · min ⁻¹	L min ⁻¹ · kg ⁻¹
SMR	1.196	−0.154	1.172	−0.125
SMR (Q10)	1.096	−0.042	1.052	−0.009
Effects on allometric scaling	Δ b	var % b		
Temperature	0.112	0.076		
Ventilation	0.321	0.263		
Body mass	1.212	0.111		
Effects of unit transformation on observed variance		Coefficient of variation		
mg · min ⁻¹		3.88		
mg · min ⁻¹ · kg ⁻¹		0.96		
L · min ⁻¹ · kg ⁻¹		0.84		
L · min ⁻¹ · kg ⁻¹ (Q10)		0.65		

acclimates to the conditions (Hughes, 1966). As organismal functions scale with the challenges faced, the focus should be put on the physical environment, and the specific challenges (and equations) it brings as scaling exponents differ depending on the level of correction of the data.

Ontogenetic dependency of homeostasis-specific thresholds

A primary assumption of DEB theory is the ‘assumption of strong homeostasis’, meaning that homeostasis is always maintained. Further assumptions are ontogenetic shifts in feeding and reproduction of animals (Sousa *et al.*, 2008). Ontogenetic shifts determine preferred habitats for fish in nature (Félix-Hackradt *et al.*, 2014); likely because the characteristic sizes of animals determine many of the challenges animals face (Andersen *et al.*, 2016). Accordingly, assimilation and maintenance are likely to shift from being either surface or volume related, to the other, during the life history of a fish.

An example of the difficulty in assigning performance to a volume or surface could be the physical movement of the animal. Locomotion sets the scene for both assimilation (feeding) and maintenance (i.e. behavioural thermoregulation and escaping predators) in ectothermic fishes. During the growth of fish, they will experience changes in what forces (inertial or viscous) that govern their ability to move (McHenry and Lauder, 2005). In larger fishes, governed by inertial forces, sustained swimming performance is related to the oxygen uptake capability of the fish (gills) (Brett, 1965; 1972). On the other hand, it is anaerobic burst swimming that limits the fish top-speed via propulsive power (white muscle) (Wardle, 1975). In contrast, for the largest of fishes, top-speed is again limited by a surface, this time due to

destructive cavitation to tissue requiring increased maintenance (Iosilevskii and Weihs, 2008). The performance of the white muscle has then been suggested to be constrained via evolution to avoid this incurrence of increased maintenance (Svendsen *et al.*, 2016). Again, the weird animal paradox of van der Meer (2016) may not lie as much in the specific assumptions, as in the assignment of traits to specific volumes or surfaces. The swimming examples should highlight, that in doing so in modelling, one is bound to miss the exceptions; the boundary conditions.

Homeostasis and its related maintenance costs cannot be assumed constant; a similar argument is formulated in Lefevre *et al.* (2017). It should be evident that homeostasis is dependent on the oxygen supply in fishes, but onset of ontogenetic shifts are also hypothesized to be determined by oxygen supply relations (Pauly, 1984). Though the last topic is questioned by Lefevre *et al.* (2017), it seems to be a causality dilemma; is metabolism constrained by oxygen transport, or is oxygen transport adapting to the metabolic needs? The general need for aquatic ventilation, that is, the onset of a ventilatory requirement, occurs at a body size of 1 mm (sphere) (Krogh, 1941). Thus, if the body size of a fish, either embryo or larvae, increases above 1 mm, the homeostatic challenge of obtaining oxygen is altered; diffusion will no longer suffice. The bottom part (left) of Fig. 3 illustrates the calculations by Krogh (1941), the lower right pane illustrates calculations of relationships between oxygen consumption and body mass. By assuming a default oxygen uptake, indicative of no constraints on metabolism, the difference to the observed average scaling can be calculated (SMR = 158 mg · min⁻¹ · kg⁻¹, a body mass of 1 g, using the best-fit equation from Lefevre *et al.* (2017): 158 · M^{-0.13}). This difference would be above zero for body sizes where the metabolism is larger than the expected default metabolism—i.e. body sizes that allow for more than an average metabolic

turnover. The peak of this difference should indicate the onset of a respiratory constraint, equalling the threshold calculated by Krogh, a body mass from which larger animals starts becoming constrained by oxygen transport. Interestingly, the calculations by Krogh (1941) exactly predict the peak of the difference curve based on data from Lefevre *et al.* (2017). As suggested by Krogh (Krogh, 1941) and Pauly (Pauly, 1981; 1984), metabolism may be constrained by oxygen transport. Regardless, as there is an observed allometric scaling of mass-specific metabolic rate (Krogh, 1941; Gillooly *et al.*, 2001; Lefevre *et al.*, 2017), the fractional allocation of energy to homeostasis must change and cannot be assumed constant (cf. DEB).

Absence of a *lingua franca*—assuming homeostasis

One pivotal point of the progression of conservation physiology of fishes as a scientific field is a collaboration between fish physiologists and ecological modellers (McKenzie *et al.*, 2016). Results (Ern *et al.*, 2014; 2015; Gräns *et al.*, 2014; Norin *et al.*, 2014; Brijs *et al.*, 2015; Raby *et al.*, 2016) questioning a theory of temperature and oxygen uptake capability (Pörtner and Knust, 2007) highlights a divergence among physiologists. The environments providing maximum power for the organism, as per Fry (1971), may not be preferable for certain fishes (Norin *et al.*, 2014). Could long term maximum power output (Lotka, 1922a, 1922b) be determined by something different than the absolute power output (Fry, 1971) as determined by physiological experiments? Answering such questions requires mechanistic approaches (McKenzie *et al.*, 2016), such as the DEB theory. In a review, investigating the applicability of assumptions of the DEB theory and their corresponding evidence in the scientific literature, it is concluded:

‘... we prove that (i) the DEB theory is fully supported by empirical biological patterns and the universal laws of physics and evolution and (ii) it is a theory on metabolic organization that is as formal as physics.’—Sousa *et al.* (2008)

However promising, it remains unclear to the authors of present paper, being physiologists, how the DEB theory accounts for maintaining homeostasis (van der Meer, 2006; 2006; Sousa *et al.*, 2008). In our opinion, homeostasis and related costs must be the maintenance costs related to living. The introductory DEB literature does not seem fully supported by empirical biological patterns; however applicable DEB models might be in different settings. Does the word *maintenance* represent the same meaning to a modeller as it does to a physiologist? The most apparent DEB paradox from a physiological point of view is that homeostasis is *assumed*, and not *maintained*, a semantical difference that could prove to be of large impact. Environmental tolerances of animals are, in one way or the other, determined by a failure of homeostasis (Fry, 1971). If the mentioned progression

should be successful, it should be of importance that a common language is agreed upon. Can the measurements physiologists carry out be utilized directly in a model, or does one part need to adapt?

The animal as a machine

Having stated a range of concerns, it is appropriate to suggest a possible solution as well. In the literature, organisms are often described theoretically as engines, that is, thermodynamic systems (Lotka, 1922a, 1922b; Fry, 1947; Von Bertalanffy, 1950). Figure 4 illustrates that for fish, as for engines, there is more to function than power output. In this experiment of thought, the idling of the engine would for fishes be the standard metabolic rate and the maximum turn-around is the maximum metabolic rate, the resulting power output is in this case then the AS (Fry, 1947; 1971). The underlying assumption is that the initial decreasing of maximum metabolic rate at higher temperatures arises from one (Pörtner and Knust, 2007; Farrell, 2016) or a range of homeostatic imbalances (Wang and Overgaard, 2007; Clark *et al.*, 2013; Brijs *et al.*, 2015; Sandblom *et al.*, 2016), leading to inherent inefficiency of the organismal system. The efficiency of a system, in this case across temperature, is by convention described as its power output (AS), divided by its power input (maximum oxygen uptake).

$$\varepsilon = \frac{AS}{MMR}$$

Given the efficiency is inherent to the system then an Effective-SMR (output from idling) can be found by multiplication of SMR and the efficiency.

$$SMR_e = \varepsilon \cdot SMR$$

An upper ‘turning point’ (pejus) for idling happens when the efficiency drops below 0.5 (Odum and Pinkerton, 1955; Odum, 1983). When transitioning into environments where the efficiency drops below 0.5, an environmental threshold, much like an ontogenetic limit, is encountered. Beyond this point, maintenance will increase dramatically (Figure 4), progressing further into such environments is unfruitful for the organism. Beyond $\varepsilon = 0.5$, maintenance allocation increases faster, as whole animal efficiency approaches 0. Thinking in the lines of whole animal efficacy, explains why Frisk *et al.* (2012) suggest their fish to be at a critical acclimation temperature at 28°C (Figure 4), even though the best-fit AS (power output) is at 76% of its maximum (An efficiency of 0.5 is also signified by AS equalling SMR, and thus factorial AS being 2). Similar results of animal functioning deteriorating at high percentages of remaining AS are not uncommon. For six species of animals relying on aquatic respiration, the average AS at maximum acclimation temperature is ($\mu \pm sd$) 78% \pm 16% with efficiencies of 0.48 ± 0.08 (Frisk *et al.*, 2012; Ern *et al.*, 2014; 2015; Claesson *et al.*, 2016; Jensen *et al.*, 2017).

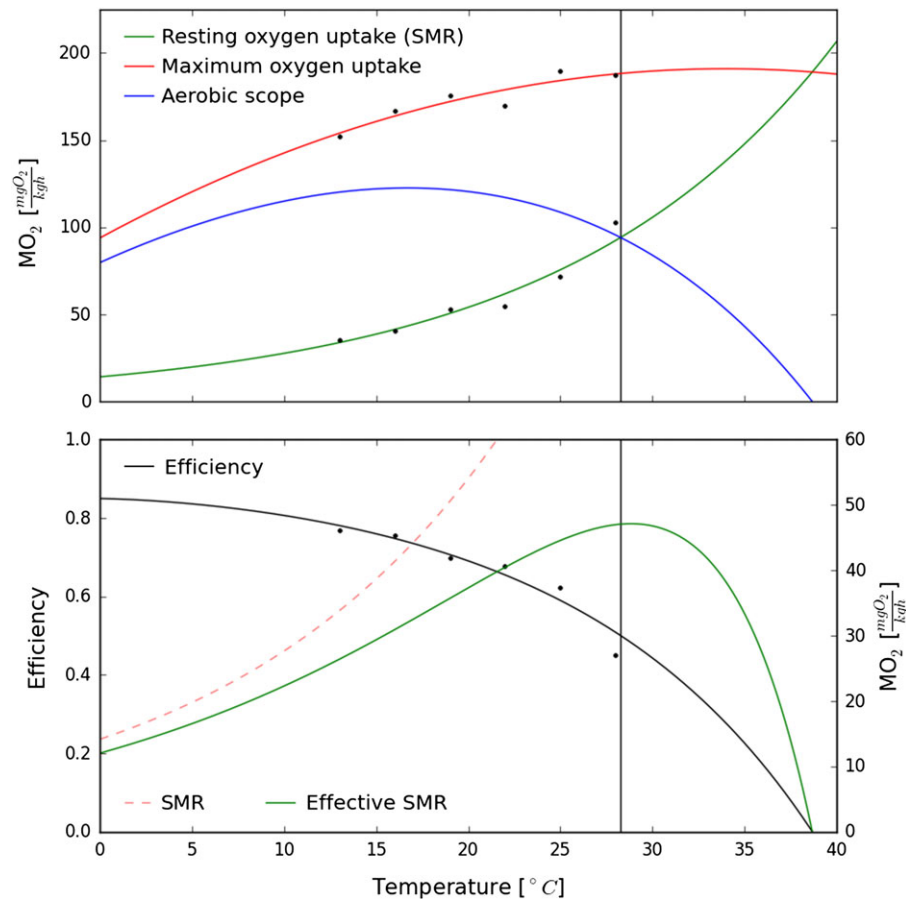


Figure 4: A fish as a machine. This example is for oxygen uptake rates (•) as proxy for metabolic rate in the freshwater fish *Sander lucioperca* from Frisk *et al.* (2012) (Top part of figure). Lines between the points represent best-fit equations (MMR: Quadratic function, SMR: Exponential). The efficacy analysis (Output/Input; see main text) is seen in the lower plot; A turning point (vertical line), where maintenance will increase radically, happens when the efficiency drops below 0.5 (AS = SMR; Factorial AS = 2). In the lower plot, the points are the calculated efficiencies (AS/MMR) of the measurements in the top plot.

Likewise, challenging fish by increasing salinity, projecting data from Behrens *et al.* (2017) indicates a 0% survival at efficiency of 0.55. Thus instead of breaking apart the animal into what specific parts are failing (Brijs *et al.*, 2015; Ern *et al.*, 2015), this simple efficacy analysis of whole animal function, explains, in part or completely, some discrepancies among fish physiologists (Ern *et al.*, 2014, 2015; Claesson *et al.*, 2016; Jensen *et al.*, 2017). Further, whole animal efficiency provides reasoning for why maximum power output, as per absolute AS (Fry, 1971), is not always the determining factor (Norin *et al.*, 2014; Claesson *et al.*, 2016; Raby *et al.*, 2016). Thus impaired performance (Gräns *et al.*, 2014) and change in preference (Norin *et al.*, 2014) is likely due to increased energy allocation to the maintenance of homeostasis. Perceiving fishes in a top-down fashion, in this case, as machines, could provide simpler mechanistic models and serve as a starting point for creating a *lingua franca* for fish physiologists; most of the references in this section are studies that criticize the oxygen

carrying capacity for thermal tolerance theory (Pörtner and Knust, 2007) and Fry paradigm, in aquatic breathers. As these differences amongst physiologists can be explained by thinking in terms of efficiency, maybe a basis for a bridge between physiologists and modellers is found in using the same terms. Hopefully creating a basis for determining the reaction norm of the effects of the environment on fishes.

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